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TRILOPHOSAURUS (ARCHOSAUROMORPHA: TRILOPHOSAURIDAE) POSTCRANIA FROM THE UPPER TRIASSIC BLUE MESA MEMBER OF THE PETRIFIED FOREST FORMATION (CARNIAN: ADAMANIAN), ARIZONA, USA

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Abstract—*Trilophosaurus* is a genus of Late Triassic archosauromorph known exclusively from the American Southwest. The defining characteristic of the taxon is its transversely arranged, tricuspid teeth. Here, we document various *Trilophosaurus* postcrania from the Krzyzanowski bonebed, NMMNH locality 3764, a multi-taxic bonebed located in the Blue Hills of Apache County, Arizona. These postcrania represent the first *Trilophosaurus* remains identified based solely on postcrania, in the absence of cranial or dental material. The *Trilophosaurus* specimens collected from NMMNH locality 3764 consist of two cervical vertebrae, two dorsal vertebrae, an incomplete humerus, a right ulna, a nearly complete right radius, an articulated left ilium and ischium, an isolated left ilium, three femora, an incomplete left tibia and an isolated right astragalus. The most prominent diagnostic character uniting the Krzyzanowski bonebed specimens and *Trilophosaurus* is the large, extensive internal trochanter on the femur and the overall morphology of the astragalus. We tentatively identify the Krzyzanowski specimens as pertaining to *Trilophosaurus* cf. *T. jacobsi* based on various shared features of the cervical vertebrae, humeri and ulnae. The presence of *Trilophosaurus* cf. *T. jacobsi* within the lowermost Blue Mesa Member of the Petrified Forest Formation is consistent with the established biostratigraphic range of *T. jacobsi*.

INTRODUCTION

Trilophosaurus is a genus of Late Triassic archosauromorph known exclusively from the American Southwest. The defining characteristic of the taxon is its transversely arranged, tricuspid teeth (Case, 1928a, b; Murry, 1987). Historically, few studies examined the postcranial morphology of the genus (Gregory, 1945; Long and Murry, 1995). However, extensive new collections of *Trilophosaurus* postcrania have been made and the classic collections have been reexamined (Heckert et al., 2006; Spielmann et al., 2007, 2008). These recent studies allowed Spielmann et al. (2007, 2008) to identify postcranial characteristics that are diagnostic of *Trilophosaurus* at the genus- and species-level (*T. buettneri* and *T. jacobsi*).

Here, we document various *Trilophosaurus* postcrania from the Krzyzanowski bonebed, NMMNH locality 3764, a multi-taxic bonebed located in Apache County, Arizona (Fig. 1). This represents the first *Trilophosaurus* remains identified in an assemblage based solely on postcrania, in the absence of isolated teeth and/or maxillary/mandibular fragments (Figs. 2-3).

GEOLOGIC SETTING

The Krzyzanowski bonebed, NMMNH locality 3764, is in the lowermost Blue Mesa Member of the Petrified Forest Formation, Apache County, Arizona (Fig. 4). It is located southeast of Petrified Forest National Park and immediately northeast of St. Johns, Arizona in an area of badlands known informally as the "Blue Hills." Vertebrate fossil collecting in the Blue Hills extends back to the 1920s (Long and Murry, 1995), with the vast majority of the recovered fossils coming from high in the Bluewater Creek Formation or low in the Blue Mesa Member of the Petrified Forest Formation (Heckert and Lucas, 2003; Heckert et al., 2005; Fig. 1).

The geology of the Krzyzanowski bonebed, NMMNH locality 3764, was summarized by Heckert (2004, p. 124) as "a thin (6-8-cm thick), well-rounded, very light gray to bluish white clay pebble conglomerate overlain by 75-80 cm of highly smectitic, purple mudstone that is heavily color mottled to various shades of gray and white. Thin sheets of dark brownish gray to greenish gray sideritic concretions cover many of the bones." He concluded that this indicated the assemblage was a channel or crevasse-splay deposit exposed to substantial pedogenesis.

TRILOPHOSAURUS FOSSILS

The *Trilophosaurus* fossils collected from NMMNH locality 3764 and thus far prepared consist of two cervical vertebrae, two dorsal vertebrae, an incomplete humerus, a right ulna, a nearly complete right radius, an articulated left ilium and ischium, an isolated left ilium, three femora, an incomplete left tibia, and an isolated right astragalus. All the material is disarticulated, but some specimens (e.g., NMMNH P-40939) were collected from a relatively small area, and should be considered associated.

Cervical Vertebrae

Two cervical vertebrae of *Trilophosaurus* have been identified; one is isolated and nearly complete (NMMNH P-60208, in part: Fig. 2A-B), while the other is part of a conglomerated mass of vertebral elements and fragments (NMMNH P-40939: Fig. 2G-H), thus obscuring some of the details of the specimen.

Both vertebrae share procoelous, single-keeled centra that are anteriorly arched (ventrally concave) in lateral view, with prominent prezygapophyses that extend beyond the anterior face of the centra and are angled medially in anterior view. NMMNH P-60208 possesses a complete neural arch and neural spine, with unbifurcated spinopostzygapophyseal laminae and a triangular, anteriorly-canted neural spine with a flat top. The neural spine does not match the neural spines of *Trilophosaurus buettneri*, which are proportionally larger and do not possess a flattened top. The Krzyzanowski bonebed vertebrae possess complete neural spines, which have an elongate base; this distinguishes them from *Spinosuchus caseanus*, which has neural spine bases that are not elongate, presumably to support more rod-like neural spines (Spielmann et al., 2009, p. 285). The procoelous centrum and lack of bifurcation of the spinopostzygapophyseal laminae are most similar to *T. jacobsi* (Spielmann et al., 2007, p. 239; 2008, p. 11-12).

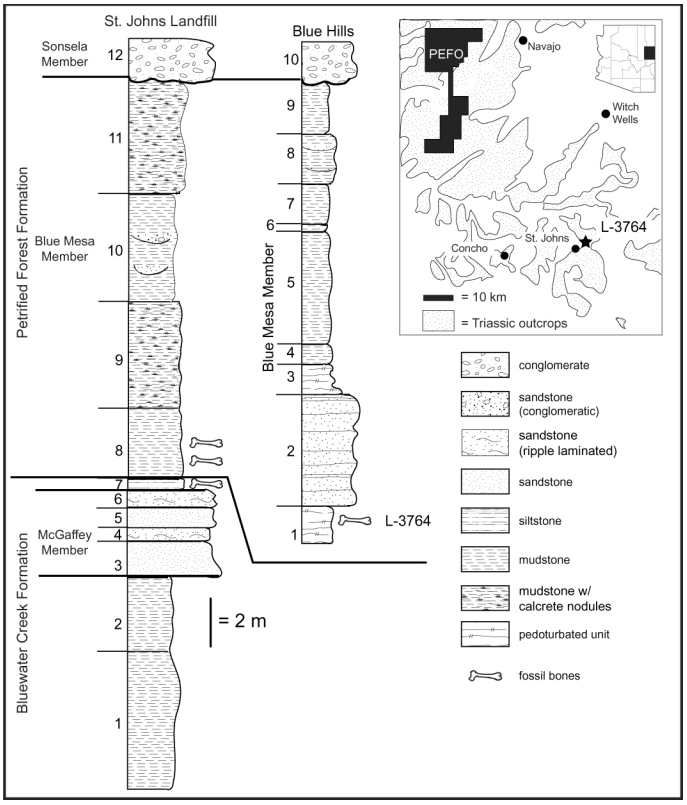

FIGURE 1. Index map and stratigraphic sections showing the location and stratigraphic position of the Krzyzanowski bonebed, NMMNH locality 3764. From Heckert (2004, fig. 104).

Dorsal Vertebrae

Two isolated *Trilophosaurus* dorsal vertebrae have been collected, NMMNH P-40937 (Fig. 2E) and P-40939 (in part) (Fig. 2C-D). NMMNH P-40937 is missing both its left and right postzygapophyses and its right transverse process. NMMNH P-40939 (in part) is missing only its transverse processes and possesses a complete triangular neural spine. Currently there are no dorsal vertebrae known for *T. jacobsi* (Spielmann et al., 2008), which complicates comparisons. However, the dorsal vertebrae from the Krzyzanowski bonebed share the following features with the dorsal vertebrae of *T. buettneri*: amphicoelous centra with single ventral keels and spinopost-zygapophyseal laminae that extend along the postzygapophyses.

Humerus

The isolated humerus assigned to *Trilophosaurus*, NMMNH P-60208 (in part) (Fig 2I-J), is very incomplete. Its proximal end is completely missing, the shaft has been torqued and the distal end is partially crushed. However, the distal end of the humerus is similar to *Trilophosaurus* in overall outline and a distinct triangular process on its ectepicondyle, which is present in *T. jacobsi*, but absent in *T. buettneri* (Spielmann et al., 2008, fig 100a-d) (Fig. 2I-J).

Ulna

A single right ulna, missing most of the proximal end, NMMNH P-63572 (Fig. 2K-L), was recovered from the Krzyzanowski bonebed. The specimen also has been partially crushed and has a postmortem kink at the midshaft. Overall the element has a similar outline to the distal ulnae of *Trilophosaurus* and shares with *T. jacobsi* a distinct spur on the ventrolateral edge of the distal ulna (Spielmann et al., 2008, p. 115, figs. 102-103) (Fig. 2K-L).

Radius

NMMNH P-60208 (in part) (Fig. 2M-N), a nearly complete right radius, is missing its distal articular surface and is slightly bowed, which is a typical preservation for *Trilophosaurus buettneri* radii (e.g., Spielmann et al., 2008, figs. 72-73). No *T. jacobsi* radii have been identified. NMMNH P-60208 (in part) has a teardrop-shaped proximal articular surface with a prominent point that extends above the level of the rest of the articulation (Fig. 2N), which is a feature also seen in *T. buettneri* (Fig. 2 M-N).

Ilia

The two *Trilophosaurus* ilia collected from the Krzyzanowski bonebed, NMMNH P-44174 (Fig. 3A-B) and P- 40939 (Fig. 3C), are of two different size classes, with NMMNH P-44174 deriving from a much larger individual than NMMNH P-40939. Both share a prominent anterodorsal acetabular rim, and an open posterodorsal acetabular margin. This is similar to the acetabular morphology of *Trilophosaurus* as illustrated in by Spielmann et al. (2008, figs. 76-77, 105-106), however, comparisons are difficult due to the only specimen of *T. jacobsi* illustrated being a juvenile. The low, triangular iliac blade with minimal anterior extension is also similar to the ilia of *Trilophosaurus*.

Ischium

The only *Trilophosaurus* ischium in the assemblage is an incomplete specimen articulated with the large left ilium (Fig. 3A-B). The anterior and ventral margins are incomplete, however, the posterior outline matches known *Trilophosaurus* ischia illustrated by Spielmann et al. (2008).

Femora

The femur of *Trilophosaurus* is one of the most distinctive postcranial elements, based on the large internal trochanter, which Spielmann et al. (2005) used to argue that *Trilophosaurus* was arboreal. The three femora collected from the Krzyzanowski bonebed all share large internal trochanters that extend one-third of the way down the femoral shaft, a key diagnostic character of *Trilophosaurus* (Spielmann et al., 2007, 2008). Two left femora (NMMNH P-60208 (in part): Fig. 3D-F, and P-63571: Fig. 3G-H) and one right femur (NMMNH P-60208 (in part): Fig. 3I-K) have been collected. Of the three, the right femur (NMMNH P-60208 (in part)) is the most complete and minimally distorted. The left femur of NMMNH P-60208 has a crushed shaft and distorted proximal end. NMMNH P-63571 is missing its proximal end, has a crushed midshaft and fragmentary distal end. Spielmann et al. (2008) noted two variations within the femora of *Trilophosaurus*: (1) the shape of the internal trochanter - a sharp triangular outline or a more rounded triangular outline; and (2) the alignment of the proximal end of the femur with the midshaft - either straight from proximal end to midshaft or with a distinct kink between proximal end and midshaft. The Krzyzanwoski bonebed *Trilophosaurus* femora all possess rounded triangular internal trochanters and straight proximal ends (Fig 3D-E, I-J).

Tibia

A single proximal left tibia (NMMNH P-44164: Fig. 3M-O) has been collected from the Krzyzanowski bonebed. The proximal end of the tibia is roughly kidney-shaped and possesses two distinct cotyles for articulation with the distal femur, as in *Trilophosaurus*. Spielmann et al. (2008) noted variation in the proximal ends of *Trilophosaurus* tibiae, based on the shape of the femoral cotyle: pointed; intermediate; and rounded. The Krzyzanowski bonebed specimens have rounded femoral cotyles (e.g., Fig. 3O).

Astragalus

An isolated right astragalus, NMMNH P-42189, collected from the Krzyzanowski bonebed can be assigned to *Trilophosaurus* (Fig. 3P-

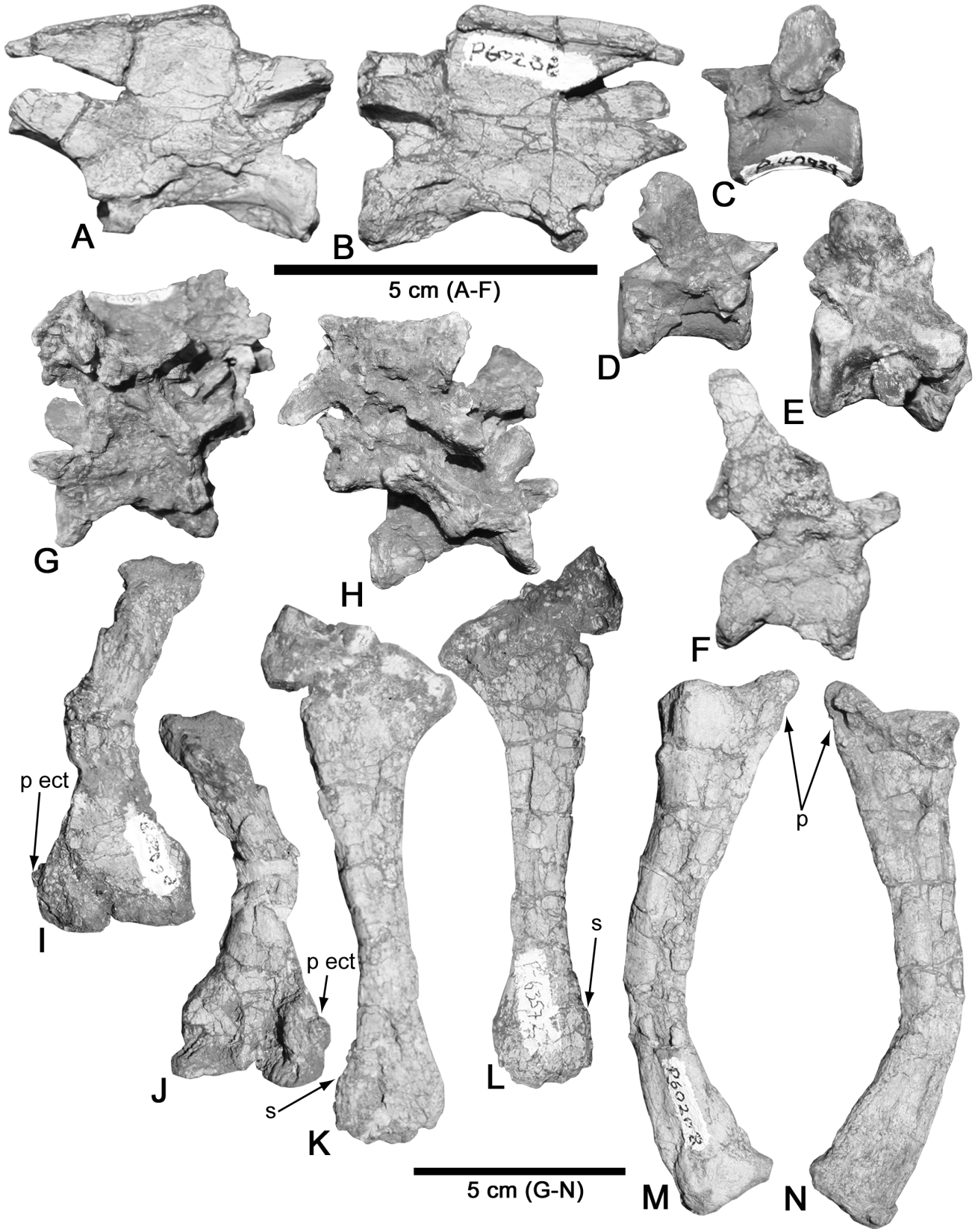

FIGURE 2. *Trilophosaurus* cf. *T. jacobsi* postcrania from the Krzyzanowski bonebed, NMMNH locality 3764. **A-B**, NMMNH P-60208 (in partim), cervical vertebra in **A**, left and **B**, right lateral views. **C-D**, NMMNH P-40939 (in partim), dorsal vertebra in **C**, left and **D**, right lateral views. **E**, NMMNH P-40937, dorsal vertebra in right lateral view. **F**, NMMNH P-60208 (in partim), dorsal vertebra in right lateral view. **G-H**, NMMNH P-40939 (in partim), conglomerated mass of vertebrae including a cervical vertebra in **G**, left lateral and **H**, right lateral views. **I-J**, NMMNH P-60208, distal right humerus in **I**, anterior and **J**, posterior views. **K-L**, NMMNH P-63572, right ulna in **K**, anterior and **L**, posterior views. **M-N**, NMMNH P-60208 (in partim), right radius in **M**, anterior and **N**, posterior views. **Abbreviations: p**, pointed articular surface; **p ect**, process on ectepicondyle; **s**, spur.

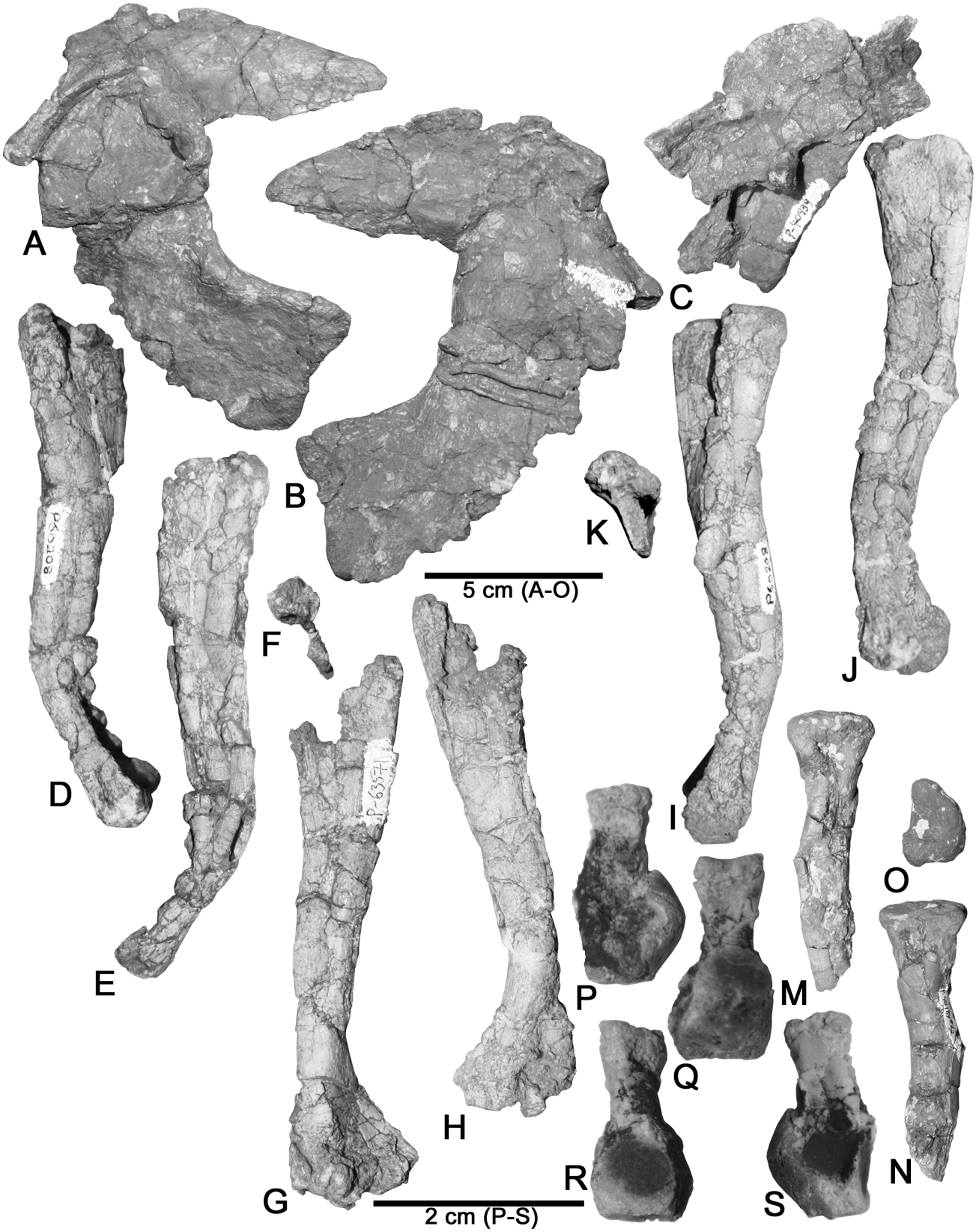

FIGURE 3. *Trilophosaurus* cf. *T. jacobsi* postcrania from the Krzyzanowski bonebed, NMMNH locality 3764. **A-B**, NMMNH P-44174, Left pelvic girdle with a nearly complete ilium and incomplete ischium in **A**, lateral and **B**, medial views. **C**, NMMNH P-40939, Small left ilium conglomerated on another bone fragment in lateral view. **D-F**, NMMNH P-60208 (in partim), Left femur in **D**, medial, **E**, lateral and **F**, proximal views. **G-H**, NMMNH P-63571, Incomplete left femur in **G**, medial and **H**, lateral views. **I-K**, NMMNH P-60208 (in partim), Right femur in **I**, lateral, **J**, medial and **K**, proximal views. **M-O**, NMMNH P-44164, Left tibia in **M**, medial, **N**, lateral and **O**, proximal views. **P-S**, NMMNH P-42189, Right astragalus in **P**, posterior, **Q**, medial, **R**, lateral and **S**, anterior views.

S). It possesses the distinct "jug"-shape of *Trilophosaurus* astragali, with a rectangular base and a neck that extends dorsally. The Krzyzanowski astragalus is comparatively thick and tall, and thus conforms more closely to *T. jacobsi* than *T. buettneri* (Spielmann et al., 2008, p. 11-12). As noted by Spielmann et al. (2008, p. 104) the astragalus is "one of the most distinctive bones of the postcranial skeleton of *Trilophosaurus*."

DISCUSSION

As noted above, fossils of *Trilophosaurus* have traditionally been identified based on cranial and/or dental specimens that bear the diagnostic tricuspid teeth for which the taxon was named (Case, 1928a, b). However, the osteologies presented by Gregory (1945) and Spielmann et al. (2008) allow for postcranial characteristics to be used for identification of *Trilophosaurus* specimens. Indeed, no dental or cranial specimens of *Trilophosaurus* have been identified from the Krzyzanowski bonebed. However, we are confident in our assignment of the specimens described above based on the numerous characters shared between this material and previously illustrated *Trilophosaurus* fossils. The most prominent diagnostic character uniting these specimens and *Trilophosaurus* is the large, extensive internal trochanter on the femora. We tentatively identify the Krzyzanowski specimens as pertaining to

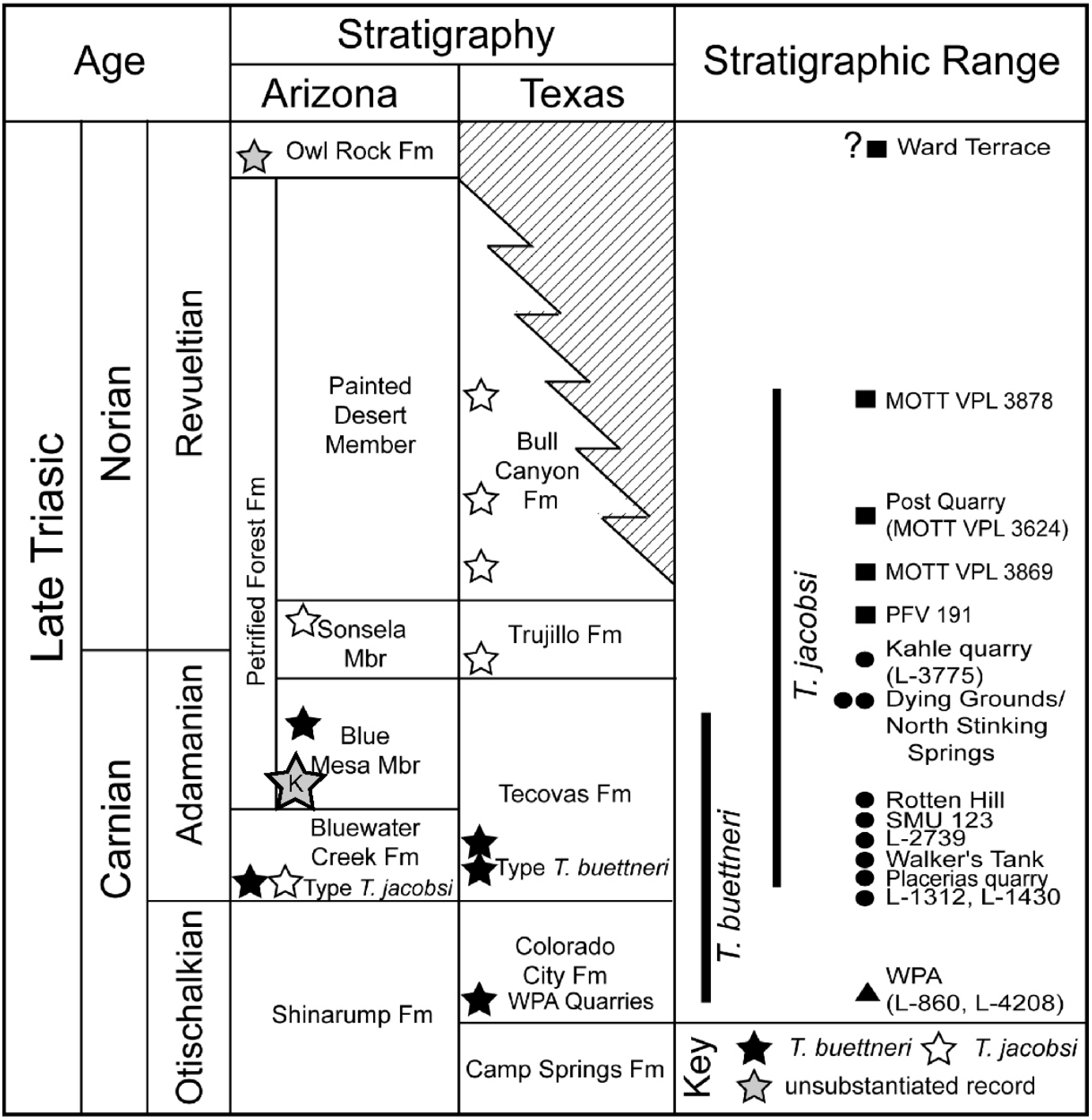

FIGURE 4. Biostratigraphic distribution of Trilophosaurus occurrences in the southwestern United States. Large gray star with a "K" in the center indicates stratigraphic position of the Krzyzanowski bonebed, NMMN locality 3764. Modified from Spielmann et al. (2008, fig. 3).

Trilophosaurus cf. *T. jacobsi* based on various shared features of the postcrania, including procoelous cervical centra and lack of bifurcation of the cervical spinopostzygapophyseal laminae, the distinct triangular process on the ectepicondyle of the humerus and the distinct spur on the ventrolateral edge of the distal ulna.

The presence of *Trilophosaurus* cf. *T. jacobsi* within the lowermost Blue Mesa Member of the Petrified Forest Formation is consistent with the established biostratigraphic range of *T. jacobsi* (Spielmann et al., 2008, fig. 3), extending from the lower Bluewater Creek Formation, which underlies the Blue Mesa Member in Arizona, through the middle Painted Desert Member of the Petrified Forest Formation (Fig 4). The use of postcrania to identify *Trilophosaurus* also allows us to emend the known vertebrate assemblage of the Krzyzanowski bonebed, in particular, and the Blue Hills, in general, to include *Trilophosaurus* cf. *T. jacobsi* (Table 1).

ACKNOWLEDGMENTS

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TABLE 1. The vertebrate fauna of the St. Johns area exclusive of the *Placerias* quarry. Uppermost Bluewater Creek Formation/Blue Mesa Member, Blue Hills, after Heckert (2004; Heckert et al., 2005).

Taxa:	
Osteichthyes:	
	Actinopterygii*
	Arganodus sp.
Amphibia:	
	Koskinonodon perfectum
	Apachesaurus sp.
Reptilia indet.	Multiple taxa*
Synapsida:	*Placerias* sp.
Archosauromorpha:	*Trilophosaurus* cf. *T. jacobsi**
	Multiple indeterminate taxa*
Archosauriformes:	Type H?*, L teeth* of Heckert (2004)
	Krzyzanowskisaurus hunti
Phytosaurs:	*Rutiodon* spp. (= *Leptosuchus*)
Aetosaurs:	*Stagonolepis* sp.
	Desmatosuchus sp.
"Rauisuchians:"	Rauisuchia indet.
	Saurosuchus sp.
	Poposaurus gracilis
Sphenosuchians:	Sphenosuchia indet.*
	Parrishia
Theropoda:	at least one taxon*
Trace fossils:	Vertebrate coprolites*

* = present at the Krzyzanowski bonebed

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